STUDIES ON THE PITUITARY BODY. II.

OBSERVATIONS ON THE PITUITARY IN DIPNOI AND SPECULATIONS CONCERNING THE EVOLUTION OF THE PITUITARY.

By MERVYN GRIFFITHS, B.Sc.
(*From the Department of Zoology, University of Sydney.*)

(Eight Text-figures.)

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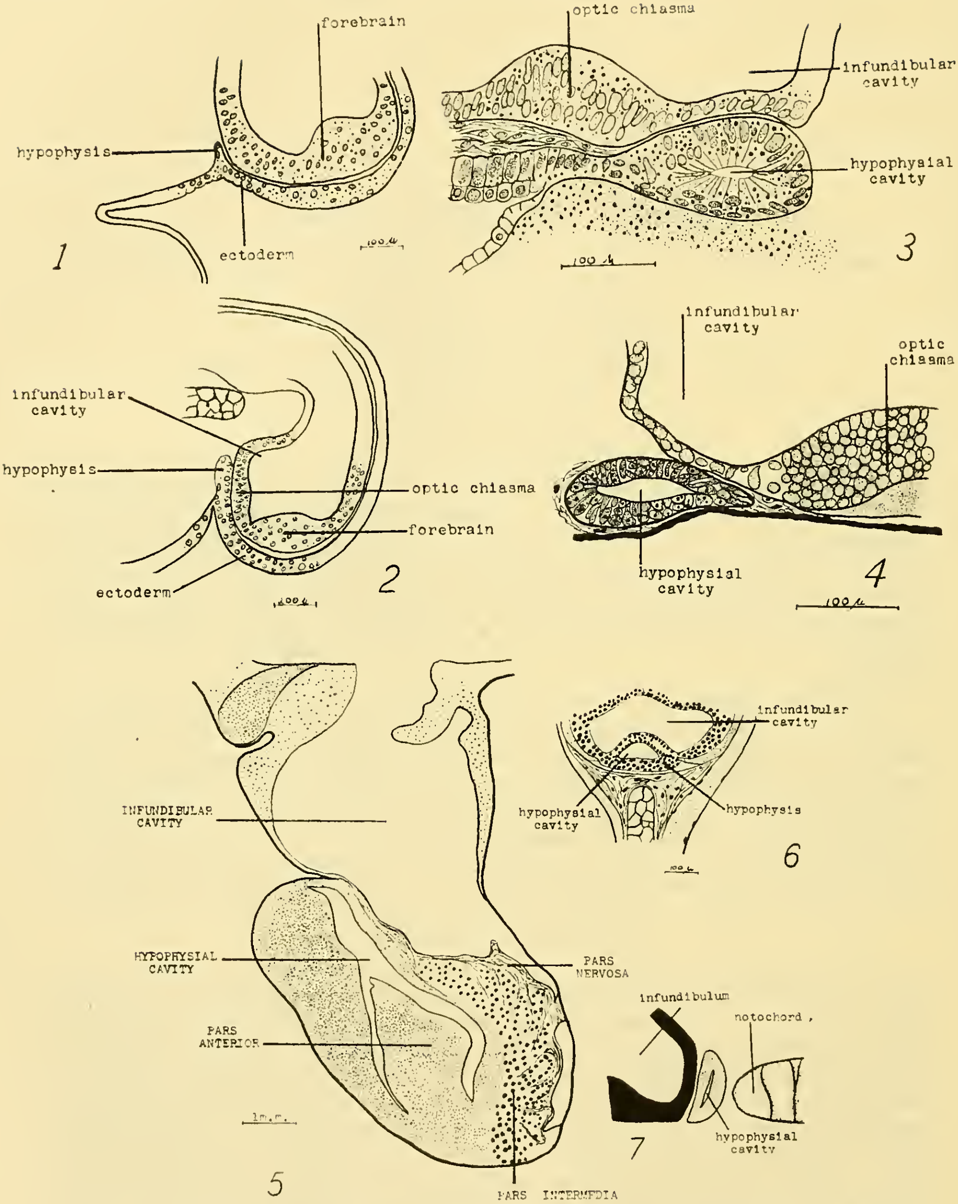
Considerable research has been carried out on the comparative anatomy and development of the pituitary body, but this structure in the Dipnoi has been practically ignored until recently. Apart from a brief description of the adult organ by de Beer (1926) and a sketch of the development by J. G. Kerr (1902) in *Lepidosiren*, the only detailed work extant is that of T. Kerr (1933), also on *Lepidosiren*. The present paper on the Australian *Epiceratodus* (*Neoceratodus*) *forsteri* and on *Lepidosiren*, is an attempt to extend our knowledge of the Dipnoan pituitary.

I wish to express my thanks to Professor E. A. Briggs, of this Department, for his advice and for the gift of the *Epiceratodus* material, and to Dr. H. L. Kesteven of Sydney for permission to examine his slides of *Lepidosiren* embryos. Complete serial sections were cut, and stained in Ehrlich's haematoxylin and eosin. The embryonic *Epiceratodus* stages were numbered according to the classification in Semon (1893). The stages examined were 32, 37, 38, 40, 42, 43, 46, 48, and one adult gland. The *Lepidosiren* material was numbered according to the stages in J. G. Kerr (1899). The stages examined were 31, 32, 33, early 36, and late 36.

The Pituitary in Epiceratodus.

Development.—The hypophysis in the earliest stage examined (32) takes the form of a small, solid conical ingrowth (Text-fig. 1) extending in from the deeper layer of ectoderm in the region of the stomodaeum, and lying between the fore-brain and foregut. By stage 37 this ingrowth has extended inwards a considerable distance, and lies beneath that portion of the forebrain immediately posterior to the rudiment of the optic chiasma (Text-fig. 2). Flexure of the forebrain is apparent at this stage. At stage 38 the ingrowth commences to expand distally. Stage 40 shows that the expanded portion has developed an eccentrically-placed cavity, situated towards the lower border of the hypophysis. By stage 42 the hypophysis has become oval in shape and the cavity central in position. As in *Lepidosiren*, the cells of the hypophysis in *Epiceratodus* are arranged in a columnar manner about the cavity, with their nuclei at the periphery (Text-fig. 3). In addition, this stage reveals a thinning of the connection between ectoderm and hypophysis. The condition in stage 43 is essentially similar to that in 42, except that the hypophysis is more circular in longitudinal section, and the connection with the ectoderm is thinner. By stage 46, the hypophysis is completely cut off



Text-figs. 1-5.—*Epiceratodus.* 1. Sagittal section of head of embryo, stage 32; anterior end to right. 2. Sagittal section of head of embryo, stage 37; anterior end to right. 3. Sagittal section of infundibulum and hypophysis, stage 42; anterior end to left. 4. Sagittal section of infundibulum and hypophysis, stage 48; anterior end to right. 5. Sagittal section of adult pituitary; anterior end to left.

Text-fig. 6.—*Lepidosiren.* Horizontal section through infundibulum and hypophysis of embryo, late stage 36. Anterior end pointing towards top of page.

Text-fig. 7.—*Protopterus.* Sagittal section of infundibulum and hypophysis of stage 33 embryo. Anterior end to left. (Copied from J. G. Kerr, 1902.)

and is seen as a small rounded body with a cavity which appears circular in longitudinal section, situated beneath the posterior end of the infundibulum. By stage 48 the hypophysis has elongated considerably, entailing a consequent elongation of its cavity. The anterior end of the hypophysis is closely appressed to the postero-ventral surface of the infundibulum just caudal to the optic chiasma (Text-fig. 4). Lateral lobes are not developed.

Unfortunately, intermediate stages between 48 and the adult were not available, but the state of affairs in the adult shows that the hypophysis, along the whole of its length, curls around and becomes intimately united to the posterior face of the infundibulum. The cells of the caudal tip become the pars intermedia, whilst growth of the hypophysis, ventral to the hypophysial cavity, results in the large pars anterior. The whole infundibulum, instead of being directed backwards, as in stage 48, grows vertically downwards into the deep sella turcica of the skull floor. Thus the gland of the adult comes to lie at a considerable distance from the optic chiasma, and the pars anterior takes up an anterior position.

Anatomy.—The adult organ is ovoid in shape, and shows no divisions externally into partes anterior, intermedia or nervosa. The relations of these divisions are shown in Text-figure 5 in sagittal section. Here it is seen that the pars anterior constitutes the main mass of the gland. Dorsally the pars anterior is attached to the membranous anterior portion of the infundibulum. At its caudal end the infundibulum thickens considerably and sends processes down into the posterior end of the adenohypophysis. This thickened region of the infundibulum is the pars nervosa. The cells of the posterior portion of the adenohypophysis are basophil and constitute the pars intermedia. The infundibulum also sends out into the pars intermedia hollow extensions which, in section, appear as open sinuses lined with ependyma. The simple elongated hypophysial cavity of the embryo has, in the adult, developed ventrally directed diverticula, extending down into the pars anterior. Two of these diverticula are seen in Text-figure 5. The hypophysial cavity in *Epiceratodus* appears to be confined to the pars anterior, and does not, as in most vertebrates, separate the pars anterior from the pars intermedia.

The cells of the pars anterior are arranged to form hollow, spheroidal vesicles which are surrounded by connective tissue. The blood supply takes the form of a richly ramifying system of fine capillaries often only of the diameter of one erythrocyte. All blood vessels are peripheral to the vesicles. A peculiar feature of the pars anterior is the presence of a colloid substance which stains with eosin, in the lumina of the vesicles. This suggests a mode of secretion similar to that of the thyroid—if indeed the colloid represents a secretion. First, the "secretion" is passed into the lumen and stored there; from here the route to the blood vessels external to the vesicle may be by diffusion through intercellular spaces in the vesicle wall or through the cells themselves.

The Development of the Pituitary in Lepidosiren.

Only five stages of *Lepidosiren* embryos were examined: 31, 32, 33, early 36, and late 36 (4·7 cm.).

At stage 31 the hypophysis, with a more or less spherical lumen, has taken up its definitive position at the posterior face of the infundibulum, and the connection with the stomodaeal ectoderm has been severed. Stage 32 shows little change from the above except for an increase in size of the hypophysial cavity. By stage 33 the hypophysis has elongated considerably, entailing an elongation of the hypophysial cavity. Early stage 36 reveals that the portion of the hypophysis ventral to the hypophysial cavity has enlarged, so that it is many cells in thickness, while the region in contact with the infundibulum is thin. A late stage 36 shows that the boundary between the infundibulum and hypophysis has broken down (Text-fig. 6).

T. Kerr (1933) says that the connection between the oral ectoderm and hypophysis breaks down at stage 27, and by stage 29 a lumen develops. But J. G. Kerr states that the hypophysial cavity develops while the connection is still present (stage 29). Probably it is safe to say that the developments in *Epiceratodus* and *Lepidosiren* are similar.

A Note on the Hypophysis in Protopterus.

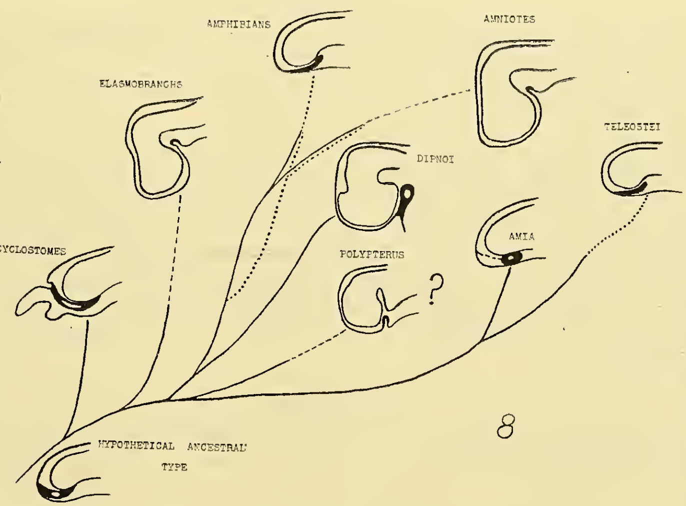
It seems from a figure given by Kerr (1902), of a sagittal section of a stage 33 *Protopterus* embryo, that the development of the pituitary in this form is similar to that of the other Dipnoans. The hypophysis at this stage bears a remarkable similarity to that in stage 33 *Lepidosiren*. Text-figure 7 is copied from Kerr's figure.

Discussion.

The hypophysis may arise as a hollow invagination (Rathke's pouch) or as a solid ingrowth. De Beer (1923, 1924, 1926) has suggested that a causal relation exists between the presence or absence of cranial flexure and the mode of development of the hypophysis. Where cranial flexure is not marked, the hypophysis arises anterior to the stomodaeum and consequently has a long distance to travel in order to make contact with the infundibulum. In all such cases (Cyclostomes, Teleostomes, and Amphibia) the hypophysis arises as a solid ingrowth. When cranial flexure is present the hypophysis arises within the stomodaeum and has only a short distance to travel in order to make contact with the infundibulum. In this case it may take the form of a Rathke's pouch (Elasmobranchs and Amniotes) or a solid ingrowth. The distance the hypophysis has to travel is the real factor concerned, a long distance ruling out the possibility of the hypophysis developing as a Rathke's pouch. In Dipnoi cranial flexure is present, consequently the hypophysis develops within the stomodaeum, but as a solid ingrowth. Now the early stages of the development of the pituitary in Cyclostomes and in Dipnoi are remarkably similar. In both, the hypophysis arises as a solid ingrowth, and in both the hypophysial cavity develops as a split within the solid ingrowth (for simplicity, I shall refer to this as a "schizo"-cavity) whilst the hypophysis is still connected to the ectoderm by a strand of tissue. But the embryonic conditions in the two groups are quite different. Cranial flexure is marked in the Dipnoi, and the hypophysis has only a short distance to travel in order to become attached to the infundibulum. In the Cyclostomes, cranial flexture is absent and the hypophysis has a much greater distance to travel. The Cyclostomes are in many respects degenerate, but they retain more primitive characteristics than any other living vertebrate, and the Dipnoi are an extremely ancient group. Therefore it is possible that the early development of the hypophysis in Cyclostomes represents the primitive mode of formation of the hypophysis and hypophysial cavity, and that this primitive mode has been retained in Dipnoi. It is hardly possible that the Dipnoi possessed the Rathke's pouch type originally and then exchanged it for the solid ingrowth, seeing that they have developed embryonic conditions favourable to the retention or evolution of a Rathke's pouch. I think it likely, therefore, that the Cyclostomes and Dipnoi have both retained the mode of early hypophysis development originally inherited from primitive ancestors which did not possess cranial flexure.

Amia, another fish retaining primitive characteristics, has the same type of hypophysis development, except that the hypophysial cavity develops after the ectodermal connection has broken off (de Beer, 1923). It would seem that the development in Teleostei and Amphibia was of this type, except that the appearance of the schizo-cavity was more and more delayed until it finally failed to develop altogether and resulted in the modern Teleost and Amphibian type. I think it likely, also, that the Rathke's pouch of Elasmobranchii, Polypterini, and Amniotes replaced independently the solid ingrowth–schizo-cavity type, due to the independent occurrence of embryonic conditions which permitted the hypophysis to develop as a pouch. Possibly, however, the pouch of Amniotes replaced the solid ingrowth–minus schizo-cavity type.

De Beer has given a tentative phylogeny of the pituitary based on the structure of the adult gland. He says, "a divergence can be traced between (i) those forms in which the hypophysial cavity disappears, the pars intermedia diminishes and the pars anterior takes up a posterior position, viz., Sauropsida and living Amphibia; and (ii) those in which the hypophysial cavity persists, the pars intermedia retains a considerable size, and the pars anterior is anterior in position". He places *Lepidosiren* in the first group, but *Epiceratodus* obviously comes into the second. The pars anterior is anterior in position, the pars intermedia is large, and the hypophysial cavity is well developed. There is no doubt that these two animals are closely related, therefore a phylogeny based on these criteria is untenable. It is obvious, also, that the hypophysial cavity in Aves and Amphibia is absent for very different reasons.



Text-fig. 8.—Scheme of evolution of the pituitary. (See text.)

I think at this stage a tentative phylogenetic table based on corresponding embryonic stages will be found useful. In the accompanying scheme (Text-figure 8) the continuous line means that the members on that line of evolution possessed the solid ingrowth–schizo-cavity type of development; the broken line indicates the possession of the Rathke's pouch which replaced the first-mentioned type; and the dotted line means that the members of this line possessed the solid ingrowth derived from the first type, but failed to produce the schizo-cavity. The development of the pituitary in *Polypterus* is not known in detail, but J. G. Kerr (1919) gives a figure of a sagittal section of a stage 32 *Polypterus* embryo, in which the hypophysis is depicted as a pouch. It is to be noted that in this scheme the distances between the points of origin of the various lines of evolution are not meant to be proportional to time intervals.

Now we must consider the question of proboscis pores (Goodrich, 1917; de Beer, 1926). Undoubtedly the proboscis pores of *Amphioxus*, Elasmobranchs, and Sauropsida are homologous. If we accept the view that Rathke's pouch replaced the solid ingrowth independently in Elasmobranchs and Amniotes, this homology of the proboscis pores needs explanation. Very probably in the earliest craniates, where the union of hypophysis and infundibulum had not evolved, the hypophysis arose as a pouch into which the cavities of the premandibular somites opened by means of proboscis pores, as happens in *Amphioxus*. Later, when the hypophysis-infundibulum combination was evolved (cranial flexure very likely being absent and the hypophysis arising anterior to the stomodaeum), the hypophysis was constrained to develop as a solid ingrowth, owing to the distance it had to travel to meet the infundibulum (de Beer has already advanced speculations similar to the above). The premandibular somites here could not communicate with the cavity of a Rathke's pouch. However, I should say, when embryonic conditions changed (independently) in Elasmobranchs and Sauropsida and permitted the hypophysis to develop as a pouch, the genes (hitherto latent) responsible for the formation of proboscis pores were able to express themselves in favourable cases.

Summary.

1. The anatomy and development of the pituitary in *Epiceratodus*, and portion of the development in *Lepidosiren* are described.

2. The similarity between the hypophyses of stage 33 *Protopterus* and *Lepidosiren* embryos is pointed out.

3. The early stages of development of the pituitary in Cyclostomes and Dipnoi are very similar, in spite of the fact that embryonic conditions in Dipnoi favour the retention or evolution of a Rathke's pouch. Reasons are brought forward to substantiate the view that the mode of development in these two groups (the solid ingrowth–schizo-cavity type) is the primitive central type from which the solid ingrowth–minus hypophysial cavity type and Rathke's pouch were derived.

4. The relation of the concept of the primitive nature of the solid ingrowth–schizo-cavity type of development, to the concept of the homology of proboscis pores is discussed.

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